THE
AMERICAN NATURALIST

VOL. XLVIII October, 1914 NO. 574

SEX-LIMITED AND SEX-LINKED INHERITANCE

PROFESSOR T. H. MORGAN
COLUMBIA UNIVERSITY

DARWIN used the expression "inheritance as limited by sex" to include all cases in which a character is peculiar to one sex. His list of such cases covers in the main the group of secondary sexual characters. Darwin's expression has been contracted to sex-limited inheritance, and is widely employed to-day in the same general sense in which Darwin used the expression. For instance, Bateson in his book "Mendel's Principles of Heredity" includes both horns in sheep and color blindness in man as sex-limited characters.[1]

Now that the inheritance of several of these cases has been definitely worked out, it has become increasingly evident that such characters as color blindness, and hæmophilia in man, the twenty-five "sex-linked" characters in Drosophila, and certain characters in birds and in butterflies follow a law of inheritance that is essentially different from that followed by some of the other cases. It has become necessary, therefore, to recognize two groups of cases that differ fundamentally in regard to their heredity. To one of these groups I have applied the term sex-linked inheritance, and, for the present at least, we may still make use of the older expression sex-limited inheritance (and

[1] See pp. 169–174 in section headed "Heredity Limited by Sex; the Horns of Sheep," where the term sex inheritance limited descent (p. 172) also appears.

sex-limited character) to cover that class of cases (obviously a very mixed one which will be broken up as our knowledge regarding it becomes more certain) that includes largely, as originally intended, the secondary sexual characters.[2] In those cases of sex-linked inheritance, in which the male is heterozygous for the sex factor, the grandfather transmits his peculiarity, through his daughters, to half of his grandsons only; and reciprocally an affected female transmits her peculiarity to all her sons, and, through her sons bred to her daughters, to half of her granddaughters and to half of her grandsons[3]. Moreover the appearance of the character in the female is not exceptional or abnormal, as is sometimes implied in cases like color blindness in man, for, the character can always be transferred from the male to the female by suitable crosses.

On the other hand, there are cases in which a character appears in one sex only—the character is limited, therefore, to the male or to the female. Such cases may be properly called sex-limited, and were so called by Darwin. As typical examples I may cite the horns of certain races of sheep that are present in the ram and absent in the

[2] G. H. Shull has recently said (*Zeit. Ind. Abst. und Vererb.*, XII, 1914, p. 160) that, in his opinion, it would be better to retain the term sex-limited for those cases that I call sex-linked and call other cases secondary sexual characters. This view is not historically in accord with Darwin's usage of the term "limited by sex." This fact, in itself would be a sufficient argument for rejecting Shull's suggestion, but, in addition, the term sex limited is an actual misnomer for the class of cases to which he proposes to apply it. There are cases like the eosin eye of *Drosophila* that differ in the male and female in the same way as do many secondary sexual characters (in fact they are such in a descriptive sense) but nevertheless show sex-linked inheritance. Since a new name is required to express our fuller information in regard to some of the characters that were originally included under the older term, why not begin by adopting suitable and expressive ones.

[3] In those cases in which the female is heterozygous for a sex factor, as in birds and in butterflies, the same principle is involved but the sequence is, in a sense, reversed; thus the grandmother transmits, through her sons, her peculiarity to half of her granddaughters; and reciprocally, the affected male transmits his peculiarity to all of his daughters, and, through his daughters bred to his sons, to half of his grandsons and to half of his granddaughters.

ewe (or else more developed in the ram than in the ewe); the color of butterflies like *Papilio Memnon,* with three types of females; and the dark spot on the abdomen of the male of the bug *Euchistus variolarius.* These characters can not be transferred through the gametes to the female of their own race by any known combination.

Whether one likes or does not like the particular terms used to denote these two classes of cases, the fact remains that there are two such categories, and to ignore their existence is only to make obscure a distinction that is perfectly plain.

Concerning the mechanism involved there is something more that may be said. It has been sufficiently shown in the case of sex-linked inheritance that the sex-linked character follows the known distribution of the sex chromosomes. It is unnecessary to repeat here the abundant evidence in support of this statement. The simplest interpretation of this known relation is that the character is dependent for its realization on the sex chromosomes. I do not mean, of course, that the sex chromosomes alone produce the character but that something in these chromosomes, some "factor," acting in conjunction with the rest of the cell, conditions the character.

On the other hand, in the case of sex-limited characters the facts can not be explained on the assumption that the characters follow the *sex chromosomes.* It is clear that they do not do so. But we can give a consistent interpretation of the facts if we assume that sex-limited characters follow the distribution of the ordinary chromosomes.

Since this relation has recently been not understood and misinterpreted I may be pardoned, I hope, for taking up the question once more.

Wood crossed horned Dorset sheep with hornless Suffolks. The sons had horns, the daughters lacked them. Inbred these gave in the F_2 generation—horned ♂, 3; hornless ♂, 1; horned ♀, 1; hornless ♀, 3. Bateson and Punnett have shown that the results are explicable on the basis that one factor for horns in the male produces

horns but one factor is insufficient in the females. This conclusion was put to the test by breeding an F_1 hornless ewe to a hornless ram. The F_1 ewe should be heterozygous for the factor for horns, and, therefore, when she is bred to a homozygous hornless ram, half of her offspring should be heterozygous for hornlessness and half homozygous for hornlessness. Since half of her sons should have a factor for horns they are expected to develop horns, and this is what occurred. Half of the daughters also should have a factor for horns, but should not develop horns, and this also was true.

It has been recognized *for several years* that this and related cases can not be explained on the assumption that the factors involved are carried by the X or by the Y chromosomes. But we can interpret the statement that one factor for horns is sufficient in the males to call forth horns, but not sufficient in the female "in terms of chromosomes," if a factor for horns is carried by one of the chromosomes other than the sex chromosome. In other words we need only appeal to a mechanism with which we are familiar to cover the results.

The second illustration is furnished by the recent experiments of Foot and Strobell, and since the authors have rejected the chromosome hypothesis as inapplicable to their results, and since in the case of insects the conditions are simplified because castration experiments have shown that the sex glands are not themselves responsible for the secondary sexual characters, we may profitably consider this case even more fully.

In one of the bugs, *Euchistus variolarius,* the male has a black spot on the abdomen. The female lacks the spot. A female of this species was crossed to a male of another species, viz., *Euchistus servus,* having no spot in either sex. The daughters had no spot, the sons had a spot fainter than that of *variolarius.* Inbred these gave, in F_2, 249 females without a spot, 107 males with a spot (developed to different degrees) and 84 males without a spot. The F_1 results show that one factor for spot in the male

suffices to call forth in some degree the spot in the hybrid. Its intensity varies from a condition approaching that in pure *variolarius* to a faint spot (possibly even to no spot at all). The F_1 results show also that a single factor in the female fails to cause the spot to develop in that sex. In the F_1 male the failure of the spot to reach in most cases its full development shows obviously that the same conditions that produce a male that is perfect so far as his sex gonad is concerned, do not suffice to cause the full development of the spot, although the factor for the spot is present in one dose at least. The only confusion that is liable to arise is that in none of the F_2 females did the spot appear, although in some of them there must have been a double dose of spot. But the difficulty is imaginary as a little thought will show. In the first place the female of *E. variolarius* herself does not show the spot, *yet this female must have a double dose of spot if spot is in the X chromosome or in any other chromosome (except the Y)*. Foot and Strobell by an elaborate analysis of the case show that the factor can not be carried by either the X or the Y chromosome. It is unnecessary to repeat their argument; for, if the factor were carried by the X chromosome, only half of the grandsons should show it, while, in fact, many more than half of them show it; and it could not be carried by the Y chromosome because the Y chromosome of *variolarius* is not present in the female, hence could not have entered the cross as made. We are concerned then only with a third possibility, viz., that there is something in the female condition itself that is inimical to the development of the spot. *Since neither X nor Y carries the factor in question it must be present in duplex in the female of variolarius (if every gamete must have it in simplex and the experiment shows that this is the case), and since the spot does not show in the female of variolarius, it is obvious that it can not appear in that sex even in duplex. If it be granted that the character is like other Mendelian characters, and the authors' evidence show that it is inherited as are Mendelian characters, the conclusion*

is self evident; for, in demonstrating that all of the gametes of variolarius carry spot the authors actually destroy their own argument.

It only remains to point out some of the different ways in which a factor being present in duplex both in the male and in the female produces its effect only in the male. In some cases it has been shown that the ovary produces some substance that is inimical to the production of certain characters. For instance in fowls and in ducks the presence of the ovary suppresses the development of the male plumage. That the factors for the male plumage are present is shown by its development when the ovary is removed. But in some insects it has been found that neither the ovary nor the testis produces these kinds of substances; for, when the testis or the ovary is removed the secondary sexual characters are not affected. Here the mode of explanation must be different. But the conditions, or complex, or factors that produce the ovary in the female are acting in every cell of the body, and consequently an effect, that is indirectly caused in the fowl or duck, might be directly caused in the insect. For, each cell is a chemical factory. Such a factory may help to produce an ovary and the ovary produce a substance that demonstrably suppresses the male plumage, or the same kind of factory may do similar work through the activity of some other part of the body, or conceivably it may do its work in every cell of the body. This it seems to me is the most reasonable view to take of the matter in the case of the *variolarius-servus* cross. We can express the same thought in symbols by representing the female of *variolarius* by XXAABBCCDDSS, etc., and the male by XYAABBCCDDSS, etc. The chemical interaction between two X's and the rest of the cell is of such kind that it produces a female, and the female complex, as such, is inimical to the development of a spot and favorable for the development of the accessory organs of reproduction and of all secondary sexual characters of the female, while XY and the rest of the cell is inimical to the development

of the acessory organs and of the secondary sexual characters of the female, and favorable for the development of the accessory sexual organs and of the secondary sexual organs of the male. This view is of course compatible with the idea that there may be special factors for these organs in chromosomes other than the sex chromosomes, and the view holds both in a general way and on the special chromosome hypothesis as well.

To assume that all the factors for characters that are shown by the male or by the female must be carried by a sex chromosome *of some kind,* if carried at all by chromosomes, is a travesty of the point of view of those who hold to the chromosome hypothesis as a reasonable working hypothesis to account for Mendelian inheritance. Just as it has been shown that there are factors in the sex chromosomes that affect many parts of the body, that are not concerned with differences of sex; so, on the other hand, the evidence shows that there are factors in other chromosomes that are influential in producing secondary sexual characters.